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THE SEASONAL DISTRIBUTION OF THE APPENDICULARIA IN THE REGION OF SAN DIEGO, CALIFORNIA

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Though microscopic or almost microscopic in size, appendicularians rank rather high in the evolutionary scale because of their alliance with the chordates, and have peculiar interest on account of their structural resemblance to certain elementary stages in development of vertebrates. Unlike sedentary tunicates which lose their tails and notochords in adult life, the appendicularians retain these structures permanently. Hence it has often happened in the past that observers have regarded them as larval forms of sedentary species. Now, however, it is well known that they constitute a distinct group, containing many genera and species, all of which are pelagic. As early as 1896 Lohmann had described eight genera and thirty-four species.

Appendicularians are pelagic tunicates belonging to the class Copelata and to the order Archipneusta. This order contains two families: Kowalevskidae and Appendicularidae. The former consists of a single genus and a single species, while the latter includes all other recorded genera and species. Since the first-mentioned family (Kowalevskidae) is rarely represented in this vicinity, it is not discussed in this paper. Discussion of the other group is undertaken under the name Appendicularians because all the past literature has appeared under the designation of Appendicularia.

The shape of an appendicularian is somewhat like that of a hammer, the short, stout body in place of the hammer head, and the long, broad tail in place of the handle. The tail is attached to the ventral side of the body at right angles and somewhat toward the posterior end. This tail, besides being the bearer of the notochord, serves also as a powerful organ of locomotion, propelling the body by its vibration.

Like all other tunicates, the animal is partly inclosed by a cellulose tunic, usually called " house " in these forms. This structure is enormously developed in all species in certain regions (mainly colder), so that not only the anterior part but the whole animal may be inclosed in it. With one exception, all species are hermaphroditic.

This paper aims to give only certain points of ecological interest concerning appendicularians, while anatomical and taxonomic features are reserved for a monograph on Pacific Coast Appendicularians, which the writer has almost ready for publication. For convenience, taxonomic reference in this article will be mainly limited to the two sub-families, Oikopleurinae and

Fritillarinae. The differences in the two groups are quite conspicuous, as may be easily seen by a glance at the accompanying figure (fig. 1).

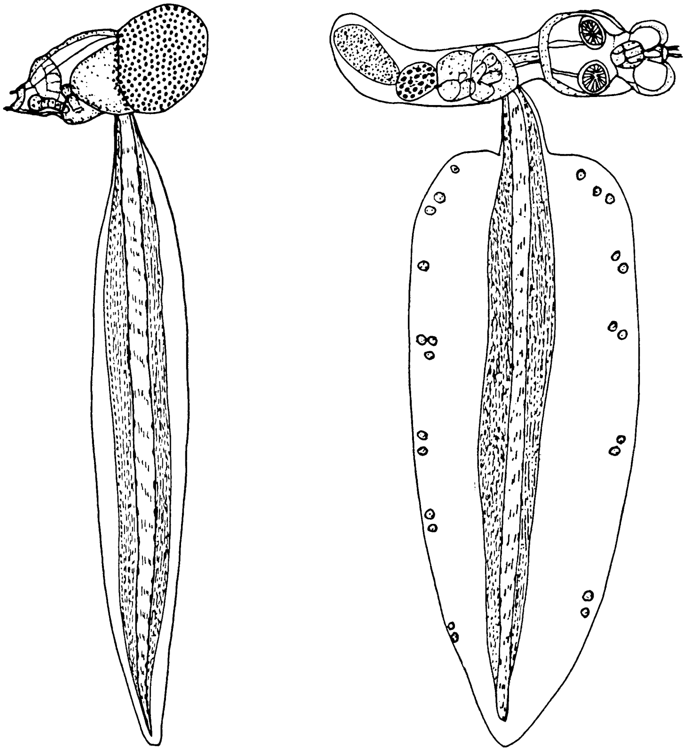

FIG. 1. Left *Oikopleura dioica;* right, *Fritillaria formica.*

Identification of species is much more difficult. Only occasional reference will be made to any particular species.

Continuous daily records of seasonal distribution of the two groups have been kept for some years, and by means of these it seems possible to identify certain interesting influences and tendencies in distribution.

Especially valuable contributions to our knowledge of distribution of appendicularians have been made by Lohmann (2) and Aida (1). At best, however, all such previous studies have been more diffuse or fragmentary than those here reported. Other studies have done little more than give geographical occurrence over wide areas, while these give an intensive view for one locality. Other conclusions have been based on very limited observations, often a single haul in each locality, but this work has been confined to a small area for a period of three years. Throughout this time daily collections have been taken from the surface of the water at or near the end of the pier at the Scripps Institution for Biological Research of the University of

California at La Jolla, California. The results summarized in the following pages are based on continuous records of observations of this material.

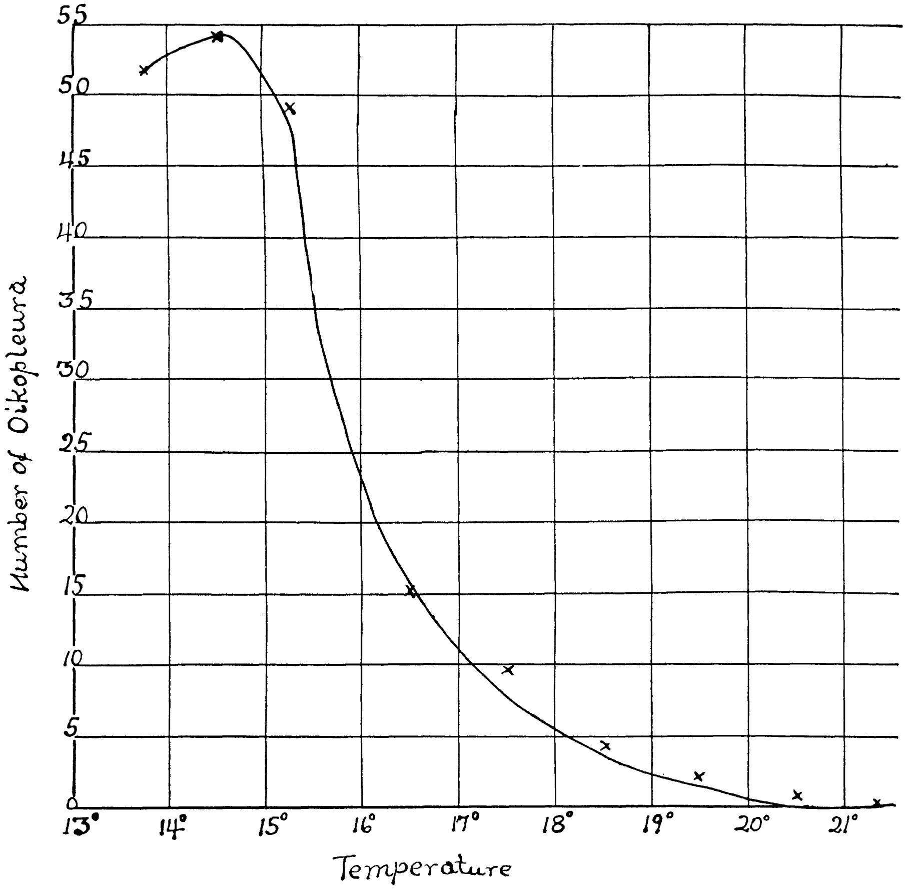

FIG. 2. Distribution of *Oikopleura* in relation to temperature of the surface water. June 1917 to March 1921.

These records show that the numbers of appendicularians are not uniformly distributed throughout the year. On the contrary, distribution varies widely with the seasons. Maximum numbers of individuals are to be found in winter, minimum numbers in summer. In fact, they are often entirely missing in warm weather. In general the data show a very marked correlation between the temperature of the water and the number of appendicularians, in which increase of temperature is accompanied by or followed by decrease in numbers and vice versa.

The average daily temperature and number of appendicularians for each month, covering the period of over three years, are given in Table 1, which gives the distribution of *Oikopleura* and *Fritillaria* in relation to temperature, and summarized graphically in figures 2 and 3.

These results point strongly to the conclusion that the distribution of appendicularians is sharply influenced by the temperature and by seasonal changes. The greatest numbers of species and individuals occur in the cooler months from October to March or April. After that the animals decrease in number gradually, until in the summer months the *Fritillaria* almost completely disappear from the surface waters, and only the cosmopolitan species of *Oikopleura* such as *O. dioica* and *O. longicanda,* with rare exceptions of other species, occur in limited numbers in that season.

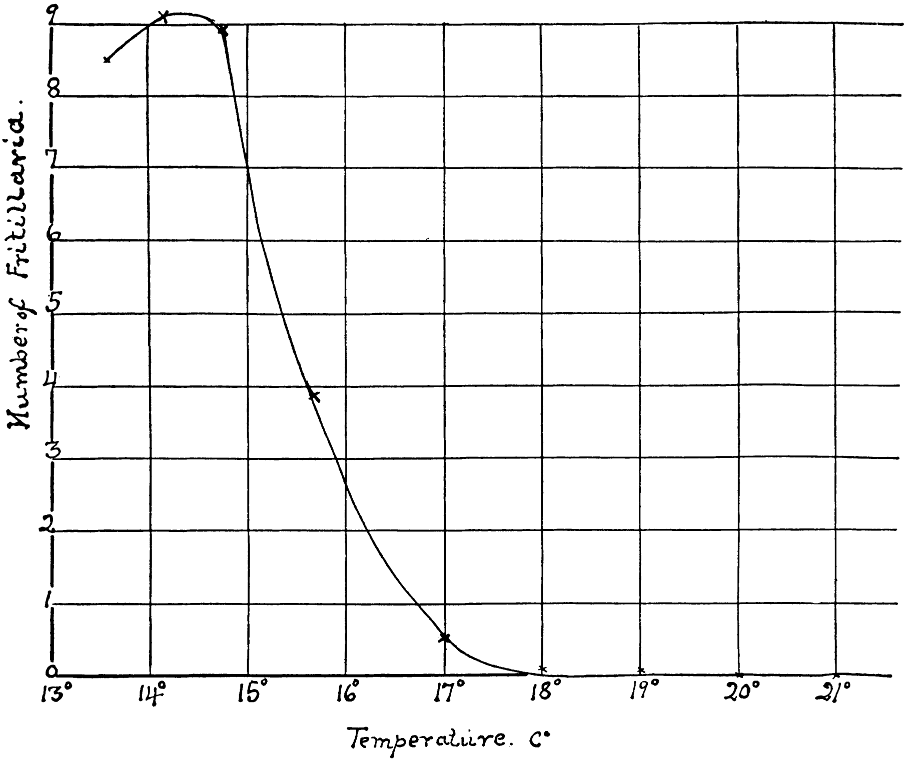

FIG. 3. Distribution of *Fritillaria* in relation to temperature of the surface water. June 1917 to March 1921.

As is shown in curves 2–3 and the table, the optimum temperature lies between 14° and 16° C. At this temperature the maximum representation is reached. In a temperature above 16° a decrease of appendicularians is noticed, and at 20°–22° they are almost completely absent from the surface waters. This is especially true of *Fritillaria,* which disappears from the surface in March or April and reappears again the following autumn in October or sometimes in the latter part of September, and is then quite abundantly

TABLE I. *Average daily temperature and number of appendicularians from June, 1917, to March, 1921*

Months	1917–1918			1918–1919			1919–1920			1920–1921		
	No. of *Oikopleura*	No. of *Fritillaria*	Temperature of surface water, Degrees C.	No. of *Oikopleura*	No. of *Fritillaria*	Temperature of surface water, Degrees C.	No. of *Oikopleura*	No. of *Fritillaria*	Temperature of surface water, Degrees C.	No. of *Oikopleura*	No. of *Fritillaria*	Temperature of surface water, Degrees C.
June	2.8	0	18.8	4.7	.087	19.9	2	....	18.78	4.8	0	19.5
July	2	0	21.3	1.95	....	21.3	1	....	21.9	3.2	0	19.03
August	5.3	....	21.5	0	....	....	2.9	....	20.5	2.5	0	21.13
September	4.5	....	19.7	2.7	....	21.8	5	....	18.4	.05	0	18.83
October	6.5	.3	17.9	5.8	.26	19.65	13	.07	18.3	20	1.5	16.97
November	21.7	7	16.3	24.6	1.56	17.3	65.6	3.05	15.9	115	6	15.22
December	37	1.8	15.5	52.3	10.84	14.9	20.7	8.8	14.5	95	2.6	13.62
January	38	2.4	13.7	61.7	17.5	14.45	51.1	.7	13.87	75.5	9.2	13.38
February	46.5	.9	13.6	73.8	28.5	14.08	15.6	8.0	14.2	16	3.5	13.11
March	15	....	14.6	167.2	18.2	13.75	77.8	11.2	14.4	16.7	2.1	14.25
April	89.8	....	15.4	50.6	6.2	14.75	42	.03	14.7	....	....	....
May	16.3	....	17.9	18.7	....	17.4	10.5	0	16.21	....	....	....

represented during the colder season. Only once during the three summers covered by the observations did *Fritillaria* occur. This was on June 14, 1918. The temperature of the water had suddenly dropped from 19° to 16°. That day the *Oikopleura* were very numerous considering the season, and among them were found two *Fritillaria.* Whether it was due to the upwelling of cold waters or to some lateral current that the temperature fell so suddenly is not certainly known, but undoubtedly the same cause that brought about a change of temperature was also responsible for the increase of *Oikopleura* and for the appearance of *Fritillaria.* It indicates that the animals dwell in either deeper water or in colder regions of higher latitudes during the hot summer months.

Reading the averages in the tables, one may get the idea that the appendicularians are equally distributed throughout the month or the season. This, however, is not the case. On the whole, species and individuals of *Oikopleura* and *Fritillaria* occur in greater abundance during the winter season, but not all the species are equally represented at the same time, various species being more prevalent than others at different times. For instance, as many as 200–300 individuals of *Fritillaria formica* in a catch were taken several days in succession. Then that species disappeared completely and has never again been taken in such abundance. Similarly other species have predominated at different times. *Oikopleura fusiformis* occurs frequently and suddenly in unusually large numbers (100–200 or more in a catch). It, too, disappears sometimes as suddenly as it appeared. The same is true of many other species. They seem to come and go sporadically, with the only difference that some species are comparatively rare and never occur in such large numbers.

One such rare species is *Appendicularia cicula.* It is seldom found in this region, hence during the first year of investigation none appeared. In the second winter three specimens were found in different catches. The last two winters it has been found again occasionally, but always in very limited numbers; two per catch has been the largest number thus far. *Appendicularia cicula* has been reported as being present in all tropical waters. It occurs in great abundance near the estuary of the Amazon River and off the West Coast of Africa, in the region of Sierra Leone. According to Lohmann, this species is usually found in surface waters in a temperature of 16°. On the African Coast, where the surface temperature is about 29.5° C., *Appendicularia cicula* dwells in deeper waters at a temperature of 11°–18°.

Kowalevskia was not found in this region until December, 1920, when five specimens of that group were taken in three different hauls within a period of four days. It has not been seen since that time. *Fritillaria pellucida* was recorded for the first time in this region in January, 1921. Only two specimens of it have been seen here thus far.

A good many other species appear more or less abundantly and irregularly at different times, so that it is impossible to know or to predict their coming or going in advance. Even the most common species of this region, such as *Oikopleura dioica* and *O. longicanda,* may appear suddenly in unusually large numbers, only to disappear again gradually or as suddenly as they came. Thus it happens that the average number of *Oikopleura* recorded as 1–2 per day, during some summer months, is not literally true, but the number was probably zero per day for the greater part of the time, the average being obtained from relatively large catches in one or two days of the month. The most satisfactory way to deal with the records would be to include the complete data here; but since that would occupy too much space, one must be content with a general idea of distribution obtained by comparing the average number of each month and season as summarized in the tables.

The aforementioned facts prove the necessity and importance of long and continuous observations on distribution. Were it not for such observation, some species would not have been discovered in this region, while others would be recorded as being abundant, especially if judged from a single catch that happened to contain an exceptionally large number of the species. Such exceptional cases are apt to lead the observer to erroneous conclusions. On the other hand, comparisons and observations of numerous collections taken from a locality regularly tend to reduce such errors, and the average data thus obtained give one a fairly good idea concerning the distribution of certain animals in a locality.

The lack of uniformity in distribution, and sudden appearance and disappearance of large numbers, leads to the question as to the explanation or cause of such conditions. Since it is impossible to follow these microscopic creatures in the vast body of water to obtain first-hand information, one may at least make a scientific guess as to what the possibilities may be.

Undoubtedly appendicularians are in existence somewhere else when they are not in the surface waters near the shores. A fair supposition is that when the temperature of the surface waters here becomes too warm the animals migrate either downward to deeper layers where the temperature is lower, or die off here while continuing to live in the surface waters of higher latitudes. One of the reasons for the uneven distribution of the different species may be that each has its particular period of reproduction. If the conditions for the development of the eggs and the young are favorable, a species may become very abundant in a locality and may be suddenly drifted to some other place by a passing current. Very little is, as yet, known about the local currents, but one has only to observe the ocean on a few calm days when their course can be seen to some extent to appreciate their importance in the distribution of the pelagic fauna.

Although no daily, continuous observations have been possible on the vertical migration of the appendicularians, a few hauls taken from deeper waters of this region in summer indicate that the animals are more abundant in deeper layers than at the surface during that season. However, these facts need more positive proofs and a more careful, systematic study.

That the distribution of appendicularians does not depend entirely on the season or the time of the year was found by a comparative study of the daily catches taken from the pier here at La Jolla and surface collections made in tropical seas at the same time, from February to April, 1920. These surface collections were made by W. C. Crandall and E. L. Michael from the yacht *Kemah* on a run from Jacksonville, Florida, to San Diego, California, by way of the Panama Canal. It is much regretted that no deep-water hauls could be taken on this trip. However, about 500 surface hauls were taken. Although appendicularians were very abundant in the surface waters of the San Diego region when these hauls were taken, they seemed to be almost completely absent from the surface of the tropical seas. However, allowance has to be made for the fact that the samples from the vessel were only about two percent as large as those from the pier. The temperature at the surface of the tropical waters varies from 16° to 29° C. Out of the 170 tropical surface hauls taken during the latter part of February and the early part of March, only thirty contained some *Oikopleura,* about 1 to 2 specimens per haul, except in 8 successive hauls, which reached fifteen to sixty per haul. *Fritillaria* were completely absent from all the hauls. Of three hundred and thirty hauls in Pacific waters, two hundred and seventeen contained appendicularians. Their number was very low in the hauls from the warmer tropical waters, but increased considerably with further advance northward into cooler waters until near San Diego, where the temperature was 14°–15°, *Oikopleura* were 100–150 per haul. From all five hundred hauls only seventeen contained some *Fritillaria.* These were all from the colder waters of higher latitudes, none being from tropical waters. Lohmann mentions some of the tropical localities traversed also by W. C. Crandall and E. L. Michael as having no *Fritillaria* in the surface waters, but he says they were abundant at a depth of 100–200 meters.

The above observations suggest that appendicularians live in surface waters as long as the temperature and other conditions are favorable for their existence, but when the temperature rises too high they seek the cooler waters in greater depths. How these animals find their way downward is unknown. Maybe by a trial and error method as Jennings found in his experiments with Paramecea. Or it may be that with the rising temperature the animals become positively geotropic and negatively phototropic, and thus move downward. In low temperatures these tropisms may be reversed and an upward movement take place. However, there is no positive proof for any such hypothesis. Some laboratory experiments on the positive and negative tropisms of the appendicularians would be of great interest if the extremely delicate condition of these animals did not render them almost entirely unfit for such experimentation. Every attempt to do experimental work with the creatures has thus far met with failure. As far as my observations go, the appendicularians do not show any tendency toward positive or negative phototropism, and when left in a dish in diffused light they do not gather on the window-side of the dish nor on the opposite side, as do many other animals with pronounced positive and negative tropisms, but remain scattered in the dish, moving in various directions.

Slight changes in light intensity do not seem to have any immediate effect on their distribution. They may be abundant in the surface waters on a bright, sunny day as well as on a cloudy or foggy day; or they may be very scarce or absent under either of those conditions. Of the few conditions under observation, the temperature seems to be the most important factor, having an immediate effect on distribution.

Next to temperature, the microplankton is to be considered as having influence of some importance, for the food of appendicularians consists of minute Protozoa, bacteria and other organisms of the kind. The water sample from the tropical regions not containing any appendicularians were also apparently void of any other organisms, so that the absence of food as well as the high temperature may be responsible for the absence of these tunicates in the surface waters. On the other hand, an excess of some of the microplankton organisms may be the cause of the disappearance of all appendicularians from the surface waters. It happens at times that such phytoplankton appears suddenly in such abundance that the water is thick and has a green or brown color and a disagreeable odor. On the first day of the appearance of this condition the appendicularians may be quite numerous, but they are sluggish, dead, or in a dying condition when they arrive at the laboratory. If the microplankton continues to exist in abundance for several days in succession, the appendicularians disappear completely from the hauls until the water is in a normal condition again. Evidently there is some poisoning effect produced by the great abundance of such microplankton in the water which exterminates the appendicularians.

Various predatory animals may be responsible for the decreasing numbers of appendicularians. As such, some of the small forms of Medusae have been frequently observed. If the latter appear in abundance with the former, medusae can be seen under a microscope attacking the appendicularians. The attack is usually begun at the tail end, and the victim is held tenaciously until the whole animal has been devoured. Similar attacks are made by Copepoda and other animals, although not so frequently. However, these are only a few of the facts that have incidentally come under my observation in the laboratory. Most of the conditions existing in the natural surroundings—the ocean—are beyond one's power of direct observation.

SUMMARY

1. The numerical results of an intensive study of appendicularians prove conclusively that the distribution of these tunicates is closely related to temperature, and that the number of individuals and species increases as the temperature decreases, and vice versa, until the optimum temperature 14°–15° C. is reached.

2. In this region the distribution of appendicularians in the surface waters is sharply influenced by the seasonal changes. With a few exceptions of some cosmopolitan *Oikopleura,* which occur occasionally in the surface waters in summer, the greater part of *Oikopleura* and all the *Fritillaria* are absent from the surface waters during that season. But all species are more or less abundantly represented in the surface waters during the winter season between October and April. However, the rich surface distribution in the winter in the San Diego region may be due to the prevailing low temperature in that season. Surface hauls taken from the warm tropical waters in the winter months were either completely devoid of appendicularians or contained very few of them, showing a condition similar to that of the summer season in this region.

3. Some past observations point to the conclusions that appendicularians migrate downward and dwell in deeper waters when the surface temperature rises too high and is unfavorable for their existence. They come back to the surface again when the temperature drops lower. These scanty observations, however, have not been verified by any intensive systematic studies.

4. Laboratory experiments on the behavior of appendicularians have been almost impossible on account of the delicate condition of the animals. But as far as laboratory observations go these tunicates do not reveal any tendency toward positive or negative phototropism. The only satisfactory results have been thus far obtained from observations in nature.

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